Running head: THIRD-PARTY EVALUATION BY TWO PRIMATE SPECIES

Common marmosets (*Callithrix jacchus*) evaluate third-party social interactions of human actors but Japanese monkeys *(Macaca fuscata)* do not

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Abstract

Reciprocity and cooperation are fundamental to human society and are observed in nonhuman primates. Primates are not only sensitive to direct reciprocity and its violation, but also indirect reciprocity. Recent studies demonstrated that some primate species adjusted their behaviour by observing others' interactions. Capuchin, marmoset, and squirrel monkeys avoided taking food from human actors who behaved non-reciprocally; however, no such empirical evidence among Old World monkeys is available. Here, we show that common marmosets, which are a highly pro-social species, discriminated between human actors who reciprocated in social exchanges and those who did not; however, Japanese monkeys, who are renowned for despotic social relationships did not. In the reciprocal condition, two human actors exchanged food equally, while in the non-reciprocal condition, one actor (non-reciprocator) ended up with all the food and the other actor with none. The common marmosets avoided receiving food from the non-reciprocator in the non-reciprocal condition. Nevertheless, the Japanese monkeys did not show differential preferences in either condition. These results suggest a crucial role for pro-social tendencies in monkeys' responses to asymmetric exchanges and indicate that third-party social evaluations are not homologous among primates. Further comparative studies with direct comparisons will be required to explore the underlying mechanism of third-party social evaluations.

Key words: social evaluation, reciprocity, marmoset monkeys, Japanese monkeys, social cognition

1

1   **Introduction**

2

3   Humans are extremely cooperative (Burkart et al., 2014; Henrich & Henrich, 2007). To

4   maintain cooperative relations, each individual should be sensitive to reciprocity, otherwise

5   freeloaders increases in the population and collapse cooperative relations in the society (Olson,

6   1965). Reciprocity is often observed in nonhuman animals (Trivers, 1971). It has been

7   proposed to explain the mechanisms for the exchange of social behaviours, such as grooming

8   in the case of primates (Molesti & Majolo, 2017). Although reciprocity is a type of altruistic

9   behaviour, especially among nonrelatives, individuals expect a return based on their own

10   actions toward a recipient. Three types of reciprocity have been proposed: direct, indirect, and

11   generalized (Molesti & Majolo, 2017). All three are possible; however, indirect and

12   generalized reciprocity seem to be limited in nonhuman primate species, at least in macaques.

13   Longtailed macaques (*Macaca fascicularis*) directed more of their grooming behaviours

14   toward those individuals that groomed them more (direct reciprocity), but not toward those

15   who groomed other individuals more (indirect reciprocity). Monkeys that received more

16   grooming did not groom others more (generalized reciprocity) (Majolo, Aureli, & Schino,

17   2011). Grooming distribution in Barbary macaques (*Macaca sylvanus*) was also

18   partner-specific (Molesti & Majolo, 2017). These results support the view that direct

19   reciprocity occurs in nonhuman primates but suggest that indirect and generalized reciprocity

20   are rare or absent in nonhuman primates. In fact, many views currently suggest that although

21   direct reciprocity was predicted to be common in nature, it is quite rare, especially 'calculated'

22   reciprocity, and the evidence for indirect reciprocity is even more limited (Hammerstein,

23   2003; Schino & Aureli, 2010).

24   Indirect reciprocity may be beneficial to altruistic individuals, because their 'reputation'

25   or 'image' increases their own probability of receiving help from others when needed (or, in

26   the case of selfishness, impairs an individual's 'image', which decreases its probability of

27   receiving help), (Nowak & Sigmund 1998; Lotem et al. 2003). Although animals may adjust

28   their behaviour in response to the presence of observers (Bshary, 2002) to improve their

29   'image', observers may also modify their behaviour based on social interactions with others.

30   The advantages to observers in social interactions are that relevant information can be

31   gathered at no risk, at little cost, and before any interactions with the interacting individuals

32   (McGregor 1993). There is growing literature regarding whether nonhuman primates respond

33   based on the observation of others' interactions (Cheney & Seyfarth 1990). So far, studies in

34   which great apes observe interactions (between humans) from a third-party stance have

35   yielded mixed results. Chimpanzees did not change their sharing/stealing behaviours

36   regardless of whether they were being watched by a group mate (Engelmann et al., 2012).

37   Chimpanzees also did not show punishment behaviours when the food of third parties was

38   stolen even when the victim was related to them, whereas they retaliated when their own food

39   was stolen (Riedl, Jensen, Call, & Tomasello, 2012). However, some studies reported, at least

40   in part, that reputational judgments resulted in a preference for cooperators (Hermann, Keupp,

41   Hare, Vaish, & Tomasello, 2013; Russell, Call, & Dunbar, 2008; Subiaul, Vonk,

42   Okamoto-Barth, & Barth, 2008). These positive results of previous studies on apes'

43   preferences for human actors who were 'generous' versus 'mean' (those who interrupted

44   food-giving) toward a third party (Russell et al., 2008; Subiaul et al., 2008) might simply

45   reflect apes' learning how to maximize their likelihood of receiving food from a human

46   (Anderson, Bucher, Chijiiwa, Kuroshima, Takimoto, & Fujita, 2017).

47   Anderson and colleagues modified procedures from previous studies of the observation

48   of others' interactions by great apes and to test capuchin monkeys (Anderson, Takimoto,

49   Kuroshima, & Fujita, 2013). They showed reciprocal and non-reciprocal exchanges by human

50   actors to capuchin monkeys. In the 'reciprocal' exchange, human actors *A* and *B* exchanged

51   small plastic balls. In the 'non-reciprocal' exchange, actor *A* picked up the balls from actor *B*;

52   however, in response to *B*'s request, *A* refused by briefly turning her head away. Thus, the

53   non-reciprocal exchange ended with *A* having all the balls and *B* none. After each of these

54   exchanges, the human actors offered food to the monkeys. The monkeys took food equally

55   from actors *A* and *B* after the reciprocal exchange. However, they avoided receiving food

56   from *A* after the non-reciprocal exchange. This study indicated that the same monkeys would

57   be sensitive to reciprocity—or more precisely, to violations of reciprocity—in exchanges of

58   items between third parties. We refer to this differential response as 'third-party social

59   evaluation'. We have replicated this third-party social evaluation with marmoset monkeys in

60   previous studies (Kawai, Yasue, Banno, & Ichinohe, 2014; Yasue, Nakagami, Banno,

61   Nakagaki, Ichihohe, & Kawai, 2015), who have well-documented pro-social tendencies and

62   cooperativeness (Burkhart et al., 2014; Burkhart, Fehr, Efferson, & van Schaik, 2007). These

63   monkeys accepted less food from human actors who failed to reciprocate in exchanges of

64   objects or food compared to actors who reciprocated.

65   So far, evidence of third-party social evaluation among primates is scarce except in

66   humans and great apes (Hermann et al., 2013; Krupenye & Hare, 2018; Russell et al., 2008;

67   Subiaul et al., 2008). It is not clear whether this is a homology among monkeys or a

68   convergence of pro-social tendencies in cooperative species. We hypothesized that primate

69   species that cooperate frequently will exhibit third-party social evaluation, because this

70   third-party social evaluation would be beneficial to species with respect to decision-making

71   such as potential partners for cooperation. In contrast, primate species that do not cooperate

72   often will not be concerned about the unbalanced outcome of others' social exchanges (Kawai

73   et al., 2014) (social system hypothesis).

74   Nevertheless, Anderson, Bucher, Kuroshima, & Fujita (2016) reported that squirrel

75   monkeys showed third-party social evaluation in their Experiment 1. This study suggests that

76   third-party social evaluation is a homology among primates, at least in New World monkeys.

77   Importantly, however, squirrel monkeys showed a biased preference for one human actor in a

78   reciprocal scenario in Experiment 2, despite no logical reason for the preference. It is not clear

79   whether the squirrel monkeys showed consistent evaluations in the two scenarios or whether

80   it was simply a randomized bias. This study used coloured balls in their exchange scenarios,

81   whereas in our studies with common marmosets, we exchanged different foods to establish

82   ecological validity. These procedural differences may generate inconsistent results.

83   One of our ultimate goals is to explore the evolutionary origins of third-party

84   evaluations and to test whether it originates in common ancestral primates as a homologous

85   psychological trait within primate lineages (homology hypothesis) or whether it

86   independently evolves as an analogous trait via socio-ecological adaptation processes (social

87   system hypothesis). Although third-party evaluation has been reported in several New World

88   monkeys and apes, less empirical evidence in Old World monkeys is available despite having

89   been long discussed in the context of social evolution. Given the critical lack of empirical

90   evidence, particularly for Old World monkeys, accumulations of comparable empirical

91   demonstrations in Japanese macaques, an ideal candidate species, would contribute to

92   ongoing debates on the primate evolution of third-party evaluation. Here, we aimed to

93   compare the common marmoset and Japanese macaque, which have different tendencies in

94   social behaviours, especially in cooperativeness and tolerance.

95   Common marmosets (*Callithrix jacchus*) are small New World monkeys that live in

96   small family groups. They are monogamous and no ranking exists within groups (Burkhart et

97   al., 2014). Common marmosets commonly give birth to two non-identical twins. Infant

98   common marmosets instinctively cling to their mother's back, and do not voluntarily let go

99   for the first two weeks. Consequently, females need help from other family members, usually

100   the father of the infants. The father takes significant responsibility for the care of the infants

101   until they are weaned at three months of age. Furthermore, individuals other than the genetic

102   parents help to care and provide for the offspring. This cooperative breeding is hypothesized

103   to be linked to improved skills in socio-cognitive and communicative processes (Burkhart et

104   al., 2014), such as concern for others, cooperation, proactive food-sharing (Jaeggi, Burkart, &

105   van Schaik, 2010), and targeted helping with non-relatives and near strangers (Burkart, Fehr,

106   Efferson, & van Schaik, 2007).

107   In contrast, social relationships among Japanese macaques (*Macaca fuscata*) are

108   considered despotic among macaque species (Katsu, Yamada, & Nakamichi, 2017;

109   Matsumura, 1999; Thierry, 2007). Macaque species are behaviourally diverse and display

110   broad interspecific variation in patterns of social behaviours. Thus, they have been arranged

111   along a 4-grade scale for social style (Reinhart et al., 2010). At one end of the scale, there are

112   grade-1 species (e.g., Japanese macaques) with highly hierarchical and despotic social

113   systems. Most social interactions among Japanese macaques are asymmetrical and reflect the

114   dominance relationship between the interactants (Chaffin, Friedlen, & de Waal, 1995).

115   Reconciliation rates in Japanese macaques are relatively low compared to rates in other

116   macaque species (Thierry, 2000), supposedly because reconciliation entails the risk of further

117   aggression. Schino, Rosati and Aureli (1998) found that Japanese macaques reconciled fewer

118   conflicts during mating season and suggested that this was because of a general deterioration

119   of social relationships resulting from increased competition and tension. A comparative study

120   of aggression and conciliation in three cercopithecine monkeys (*Macaca fuscata*, *Macaca*

121   *nigra*, and *Papio papio*) found that the use of peaceful interventions in conflicts was common

122   in crested macaques, rare in Guinea baboons, and unobserved in Japanese macaques (Petit,

123   Abegg, & Thierry, 1997). Other comparative studies have shown that whereas low levels of

124   social tolerance, marked submission behaviour, and strict hierarchies characterize Japanese

125   macaques (Aureli, Das, & Veenema, 1997; Chaffin, Friedlen, & de Waal, 1995; Kutsukake &

126   Castles, 2001; Schino, Rosati, & Aureli, 1998; McKenna, 1980), crested macaques display

127   greater tolerance and relaxed dominance (Petit, Bertrand, & Thierry, 2008). In contrast, at the

128   other end of the scale, grade-4 species (e.g., Tonkean macaques) have more relaxed and

129   egalitarian social systems (Reinhart et al., 2010). Reinhart et al. (2010) compared the play

130   fighting of Japanese (grade-1) and Tonkean (grade-4) macaques. They found that Tonkean

131   macaques exhibit a relatively cooperative style of play fighting, whereas Japanese macaques

132   exhibit a relatively competitive style of play fighting.

133   To our knowledge, Japanese macaques hardly cooperate to obtain food. In an

134   exceptional report, Kaigashi and colleagues (2016) set up a cooperative problem-solving task

135   for two groups of free-ranging Japanese macaques (Kaigaishi, Yamada, & Nakamichi, 2016).

136   Although the groups of monkeys of the Awaji Island, renowned for their high levels of

137   tolerance and low aggression, sometimes succeeded in a rope-pulling task in which two

138   individuals spontaneously approached a device to pull both ends of a single rope

139   simultaneously to retrieve a food reward, in more than half of the 1488 trials over seven

140   months. Only one individual learned to wait for a potential partner when another individual

141   was absent at the other end of the rope. The other typical group of Japanese macaques (from

142   Katsuyama) succeeded in this task in only two trials among a total of 199 trials over four

143   months. Thus, as evident in their spontaneous social interactions (reviewed above) as well as

144   their performance in this experimental task, Japanese macaques are one of the most despotic

145   macaque species and often intensely compete with others for food (Kaigashi et al., 2016).

146   To test one of the predictions derived from the homology hypothesis, we examined

147   whether Japanese monkeys evaluate the third-party social interactions of humans in a direct

148   comparison with common marmosets using equivalent procedures. Excluding the size of the

149   apparatus, food to be exchanged and provided, and human actors, the experimental variables

150   such as the order of the non-reciprocators' locations, order of trials within sessions and of

151   sessions, and so on were identical. Based on the homology hypothesis, both Japanese

152   macaques and common marmosets would avoid the non-reciprocator. In contrast, because the

153   ability to avoid non-reciprocators in third-party interactions is derived from their social

154   behaviours, the social system hypothesis predicted common marmosets, but not Japanese

155   macaques, would avoid the non-reciprocator.

156

157   **Method**

158   *Subjects*

159   Four female common marmosets (*Callithrix jacchus*) ranging in age from 5.0 to 6.5

160   years in the National Institute of Neuroscience and five female Japanese monkeys *(Macaca*

161   *fuscata)* ranging in age from 8 to 11 years in the Primate Research Institute, Kyoto University

162   were used in this experiment. Each of the four common marmosets (*Callithrix jacchus*) had

163   previously participated in a third-party social evaluation study (Kawai et al., 2014; Yasue et

164   al., 2015) and in an inequity aversion study (Yasue et al., 2018). They were cared for by their

165   parents in a pair cage until the weaning period (3 months old), and then lived in another pair

166   cage with their littermate until the age of about 1.5 years. They were subsequently housed

167   individually in cages. All the Japanese monkeys (*Macaca fuscata*) were born in social groups

168   and raised until the age of 3 at the Primate Research Institute of Kyoto University; they were

169   subsequently housed individually in cages. No monkeys had experienced cooperation and

170   reciprocity with conspecifics, but engaged in computerized tasks (Kawai & Koda, 2016;

171   Kawai, Kubo, Masataka, Hayakawa, 2016). The common marmosets and the Japanese

172   monkeys had similar social experiences as to cooperation and interaction with conspecifics.

173   The monkeys in each institute were housed in the same animal room. They could see

174   other monkeys and hear the others' vocalizations in the same room with restricted direct

175   interactions. They had free access to water and were fed monkey pellets and supplementary

176   food (including steamed sweet potatoes, pieces of bread, bananas and other fruits as well as

177   various vegetables) twice a day. The experiment was conducted prior to the second feeding,

178   twice or thrice a week.

179   *Ethics*

180   All procedures for common marmosets were performed in accordance with the National

181   Institute of Health Guidelines for the Care and Use of Laboratory Animals of Japan and were

182   approved by the Animal Research Committee at the National Institute of Neuroscience in

183   Japan. All procedures for Japanese monkeys were approved by the ethics committee of the

184   Primate Research Institute of Kyoto University and were in accordance with the Guide for the

185   Care and Use of Laboratory Primates.

186 *Procedure*

187   Because common marmosets and Japanese monkeys differ in body size, the apparatus

188 were differently sized but functionally equivalent. Prior to the experiment, all monkeys

189 voluntarily entered the apparatus with wire walls (25 × 20 × 18.5 cm for common marmosets

190 and 54 × 41 × 46 cm for Japanese monkeys) from their home cage and were taken to the

191 experimental room.

192   The experimental procedure for the third-party reciprocal/non-reciprocal exchange was

193 the same as that used in the previous common marmoset study (Yasue et al., 2015) and

194 squirrel monkey study (Anderson et al., 2016), in which one actor played one role throughout

195 the session. To initiate a trial, two female human actors opened an opaque screen, which was

196 located next to the wire wall. Manipulation of the screen was achieved using ropes and

197 pulleys by the combined effort of both the actors. Two actors (*A* and *B*) stood about 92 cm

198 from the monkey and 50 cm apart. After confirming that the monkey's attention was directed

199 towards the actors, the demonstration began in accordance with one of two conditions

200 (reciprocal condition and non-reciprocal condition). In each condition, two small pieces of

201 two types of food (steamed buns and potatoes for common marmosets, and apples and raisins

202 for Japanese monkeys) were placed on a table in front of each actor. These foods were used to

203 draw the monkey's attention and to simulate a naturalistic situation (i.e., food sharing). First,

204 actor *B* picked up the two pieces of food (food-*B*) on the table in front of *B* and showed them

205 to the monkey. Actor *A* then took the food-*B* from actor *B*'s hands and put them in front of *A*.

206 At this moment, actor *B* neither offered food to actor *A* nor rejected her action. Next, in the

207 reciprocal condition, actor *A* picked up the two pieces of food-*A* on the table and showed

208 them to the monkey. Actor *B* took the food-*A* from the actor *A*'s hands in the same way as

209 actor *A* did previously. Thus two types of exchanges were made between *A* and *B*. In the

210 non-reciprocal condition, actor *A* picked up the two pieces of food-*A* on the table. When actor

211 *B* approached the food-*A* in actor *A*'s hands, actor *A* did not allow *B* to take the food by

212 turning its back to *B*. Thus, *A* ended up with four pieces of food and *B* with none (Figure 1).

213   Actor *A* piled the food items on her pile. After each of these demonstrations, two actors pulled

214   ropes simultaneously, and the screen was closed and the food items were hidden. Five

215   seconds later, the screen was re-opened and two actors presented a reward (a piece of sponge

216   cake for common marmosets and a piece of peanuts for Japanese monkeys) in front of the

217   monkey 10 cm apart. When the monkey took one of the rewards, or monkey did not take

218   either of rewards for 20 sec., the screen was closed and the inter-trial interval of 10 s began

219   (Figure 1). The actors did not look at the monkey when they offered rewards. During

220   exchanges, the experimenters looked at their own food items or the other's food items when

221   they reached for the other's food items. When they offered food to the monkeys, they did not

222   gaze at the monkey, but looked at the area near the opened screen above the monkey. Their

223   offerings were synchronized without any vocalization.

224   The combinations of food and actors' locations were counter-balanced within each

225   session and each session contained 12 trials. As in the previous studies (Anderson et al., 2013;

226   Yasue et al., 2015), one actor failed to reciprocate 12 times in a row. Eight reciprocal sessions

227   and eight non-reciprocal sessions were conducted alternately. The actor's role was fixed in a

228   session, but changed randomly across sessions as in the previous common marmoset study

229   (Yasue et al., 2015) and squirrel monkey study (Anderson, et al., 2016). Data were pooled for

230   each individual for the statistical analyses.

231

232   **Results**

233   *Experiment 1: Common marmoset monkeys*. In 8 trials out of a total of 768 trials, the

234   common marmosets failed to take a reward from either actor, and were excluded from the

235   analysis. As shown in the left panel of Figure 2 (Figure 2), the common marmosets'

236   preference for accepting the reward did not differ between the two actors (*A* and *B*) in the

237   reciprocal condition (mean 52.08, 95% CI [55.62, 48.55] and 47.14, 95% CI [50.07, 44.20],

238   respectively). In contrast, the common marmosets showed a significant avoidance for actor *A*

239   (the non-reciprocator) over actor *B* (the reciprocator) (mean 40.10, 95% CI [45.28, 34.93] and

240   58.59, 95% CI [63.26, 53.93], respectively). An analysis of variance (ANOVA) exhibited the

241   main effect of condition, $F(1, 3) = 11.26$, $p = .0439$, partial $\eta^2 = .789$, and a significant

242   interaction of condition and actor, $F(1, 3) = 10.22$, $p = .0495$, partial $\eta^2 = .773$. However, the

243   main effect of actor was not significant, $F(1, 3) = 0.16$, *n.s.*, partial $\eta^2 = .051$. A post-hoc

244   analysis with Bonferroni correction revealed that the common marmosets accepted food less

245   frequently from actor *A* than from actor *B* in the non-reciprocal condition, $F(1, 3) = 14.07$,

246   adjusted $p = .0331$, partial $\eta^2 = .824$, and received food marginally less frequently from actor

247   *A* in the non-reciprocal condition than from actor *A* in the reciprocal condition, $F(1, 3) = 8.58$,

248   adjusted $p = .0610$. They accepted food more frequently from actor *B* in the non-reciprocal

249   condition than actor *B* in the reciprocal condition, $F(1, 3) = 11.90$, adjusted $p = .0409$, partial

250    $\eta^2 = .799$.

251   *Experiment 2: Japanese monkeys*. In 11 trials out of a total of 960 trials, the Japanese

252   monkeys failed to take a reward from either actor, and were excluded from the analysis. The

253   patterns of the results were remarkably different from those of the common marmosets. The

254   Japanese monkeys received food equally from the two actors not only in the reciprocal

255   condition (mean 50.83, 95% CI [53.75, 47.92] and 48.33, 95% CI [50.53, 46.13],

256   respectively) but also in the non-reciprocal condition (mean 50.21, 95% CI [52.19, 48.23] and

257   48.33, 95% CI [49.99, 46.67], respectively). An ANOVA revealed that the main effect of

258   actor, $F(1, 4) = 1.00$, *n.s.*, main effect of condition, $F(1, 4) = 3.25$, $p = .15$, *n.s.*, and the

259   interaction of actor and condition, $F(1, 4) < 1$, *n.s.*, were not significant.

260   A three-way ANOVA revealed that the main effects of species, $F(1, 7) < 1$, *n.s.*, η^2

261    $= .041$, condition, $F(1, 7) < 1$, *n.s.*, $\eta^2 < .001$, and actor, $F(1, 7) = 4.17$, $p = .080.$, $\eta^2 < .001$,

262   were not significant. The interaction of species and condition was not significant, $F(1, 7) < 1$,

263   *n.s.*, $\eta^2 < .001$. Nevertheless, both the interaction of species and actors, $F(1, 7) < 15.94$, p

264    $= .005$, $\eta^2 = .154$, and the interaction of condition and actor, $F(1, 7) < 10.84$, $p = .0132$, η^2

265    $= .278$, were significant. Furthermore, a second-order interaction between actor and condition

266   was also significant, $F(1, 7) < 9.74$, $p = .0168$, $\eta^2 = .250$, indicating that the common

267 marmosets made different responses to the actors in the two conditions, while the Japanese

268 monkeys did not respond differentially to the actors in the two conditions.

269   We also performed a generalized linear mixed model (GLMM) fitting for the

270 actor-choice data, considering species (common marmoset or Japanese macaques), session

271 orders, trial orders nested in session orders, and reciprocal conditions (reciprocal or

272 non-reciprocal) as fixed effect terms, with subject as a random effect term, and evaluated the

273 models by the model selection procedure. In the model, choice data were treated as binary

274 data (1: = 'actor A choice' or 0: = 'actor B choice'). First, we constructed full models that

275 included all fixed effect terms and the possible interaction effect terms. The binomial family

276 with the logit link function were used in the models. The intercept of the model was set to the

277 marmoset and non-reciprocal conditions. Next, we eliminated the fixed effect terms by the

278 stepwise model selection procedures based on the Akaike Information Criterions (AICs).

279 Subsequently, we reported the best model (the minimal AIC model) with the estimated

280 parameters. The models were fitted by the 'glmer' method in the 'lme4' package, and model

281 selection was performed by the 'dredge' method in the 'MuMIn' package in R. The 95

282 percent confidence intervals of the estimated parameters were computed by the 'confint'

283 method in the 'lme4' package.

284   The best model (AIC: 2364.4) included the reciprocal condition, species, and its

285 interaction (reciprocity and species), and all these terms were positive effects. Session order

286 was not included in the best model, suggesting no statistical explanatory power of session

287 progress in the data sets (for the details of model selections, see supplementary online

288 materials, S1). In the best model, the parameters of the interaction effect term of condition

289 and species, condition effect term, and species effect term were estimated as -0.467 +/- 0.196,

290 0.479 +/- 0.146, and 0.417 +/- 0.139 (mean +/- SD), respectively. These parameters were

291 significantly differed from 0 (condition x species, z-value = -2.38, p = 0.01716; condition,

292 z-value = 3.27, p = .00108; species, z-value = 3.27, p = .00108, supplementary online

293 materials, S2). We subsequently evaluated the estimated parameters in the best model for

294   each species. In the marmoset experiment, the estimated parameter of the non-reciprocal

295   condition was -0.38 (95% CI: -0.59, -0.18), while that of the reciprocal condition was 0.10

296   (95% CI: -0.39, 0.59). This suggested that the common marmosets likely chose actor B in the

297   non-reciprocal condition, but showed no biased choice in the reciprocal condition. In contrast,

298   the estimated parameter for the Japanese macaques in the non-reciprocal condition was 0.04

299   (95% CI: -0.44, 0.52), while that for the reciprocal condition was 0.05 (95% CI: -1.10, 1.20),

300   thereby suggesting no biased actor choice in both the reciprocal and non-reciprocal conditions

301   among the Japanese macaques.

302

303   **Discussion**

304   The present results clearly demonstrate the species difference in social evaluations; the

305   common marmosets, a pro-social species (Burkhart et al., 2014; Yasue et al., 2015; 2018),

306   were less likely to obtain food from non-reciprocal human actors when they observed an

307   asymmetric exchange between third parties who had no direct relevance to the common

308   marmosets, whereas the Japanese monkeys, a despotic species (Matsumura, 1999; Thierry,

309   2007; Katsu, Yamada, & Nakamichi, 2017), did not exhibit any differential behaviour in the

310   two conditions. This is the first demonstration that a primate species was equally likely to

311   obtain food from reciprocal and non-reciprocal human actors. These results indicate that the

312   evaluation of third-party reciprocity by monkeys is not a general trait shared with all primate

313   species. Rather, the present results suggest that primates' social evaluations of individuals

314   based on third-party interactions are the result of convergent processes, rather than homology

315   (Kawai et al., 2014).

316   The response rates by the common marmosets in the present study were quite similar to

317   those of previous studies with common marmosets and capuchin monkeys: Capuchin

318   monkeys took food more frequently from B (57.7 %) compared to A (42.3 %) in

319   non-reciprocal condition, while their responses were indifferent to both actors (B : 47.6%, A :

320   52.4 %) in reciprocal condition in Experiment 1 (Anderson et al., 2013). Squirrel monkeys

321   were more likely to take food from B (58.3 %) compared to *A* (41.7 %) in non-reciprocal

322   condition. In contrast, they showed no preference for food offered by both actors (*B* : 47.9 %,

323   *A* : 52.1 %) in reciprocal condition in Experiment 1. In Anderson et al.'s (2013) Experiment 2,

324   in which mixed trial sessions were conducted as in Kawai et al. (2014), squirrel monkeys took

325   food more often from *B* compared to *A* (58.6 % vs. 41.4 %) in non-reciprocal condition.

326   Nevertheless, they received food significantly more frequently from *A* than *B* (55.6 % vs.

327   44.4%) in reciprocal condition (Anderson et al., 2016). Marmoset monkeys were more likely

328   to take food from B (58.9 %) compared to *A* (41.1%) in non-reciprocal condition, while they

329   showed no preference for food offered by both actors (*B*: 50.2%, *A*: 49.8 %) in reciprocal

330   condition (Kawai et al., 2014). These patterns of the results were quite similar to those of

331   Yasue et al. (2015), who tested common marmosets (*B*: 59.0 % vs. *A*: 39.6 % in the

332   non-reciprocal condition; *B*: 50.9 % vs. *A*: 47.7 % in the reciprocal condition).

333   So far, common marmosets (Kawai et al., 2014; Yasue et al., 2015) have repeatedly

334   demonstrated that they were less likely obtain food from non-reciprocal human actors, while

335   they respond equally to reciprocal human actors. Two possible explanations might account for

336   the differences between the two species. The first possibility is that the lack of prior

337   experience with this test might have yielded non-differential behaviours in the Japanese

338   macaques. Monkeys experience humans giving food to them. Otherwise, they would not want

339   to interact with humans that may not give them food. The common marmosets in the present

340   study experienced this test once (Kawai et al., 2014; Yasue et al., 2015). Nevertheless, the

341   common marmosets avoided non-reciprocal actors in the first experiment. Importantly, these

342   tests were not discrimination learning tasks using differential reinforcement. Monkeys could

343   receive the same food, regardless of their choices. Furthermore, as both the actors took the

344   role of the non-reciprocator in this study, it seems unlikely that the monkeys modified their

345   behaviour based on the associations between reward contingency and specific actors. They

346   did not have any reason to modify their behaviours to avoid non-reciprocal actors. In fact,

347   they did not change their responses according to their experiences. The GLMM analysis

348   revealed that the session order was not a critical factor for explaining the present pattern of

349   the results.

350   The other possibility is that a primate species that cooperates with other conspecific

351   members will be sensitive to reciprocal interactions and its violations, while a primate species

352   that does not cooperate (i.e., reciprocal exchange) in its natural environment will not, because

353   cooperation is contingent on the nature of previous interactions among partners (Jaeggi,

354   Burkhart, van Schaik, 2010; Silk, 2015). If an individual repeatedly fails to cooperate, then

355   the opportunity to be a potential cooperation partner will be lost (Brosnan & de Waal, 2014;

356   Olson, 1965). In other words, cooperative primates have to monitor whether exchange

357   between partners is balanced. Both common marmosets (Burkhart et al., 2007; 2014; Jaeggi et

358   al., 2010) and capuchins (de Waal & Berger, 2000; de Waal, Leimgruber, & Greenberg, 2008)

359   cooperate both in experimental settings and their natural environment (Yamamoto, Box,

360   Albuquerque, & Arruda, 1996; Rose, 1997). However, the sensitivity to third-party interaction

361   may be different depending on the test used in the study. Brosnan & de Waal (2009), using a

362   different procedure, found that capuchins are insensitive to the actions of human

363   experimenters: the capuchins failed to choose the experimenter who did not cheat them over

364   the experimenter who did (see also Engelmann et al., 2012; Riedl et al., 2012). Nevertheless,

365   at least some apes respond by preferring the non-cheating experimenter (Russell, Call, &

366   Dunbar, 2008; Subiaul, Vonk, Okamoto-Barth, & Barth, 2008). In contrast, Japanese

367   monkeys do not cooperate to solve instrumental tasks as capuchins and common marmosets

368   do (Katsu et al., 2017).

369   The overall results were not driven by a strong preference by some of individuals, but

370   rather were achieved by a consistent preference among all the common marmosets. All four

371   common marmosets showed a bias toward actor *B* (the predicted direction) in the

372   non-reciprocal condition, while two out of four (50%) showed a preference for actor *B* in the

373   reciprocal condition. In the Japanese macaque experiment, three out of five monkeys showed

374   a predicted direction bias with two ties in the non-reciprocal condition, while two out of five

375   showed a preference for actor *B* with one tie in the reciprocal condition.

376   As all the common marmosets and Japanese macaques in this study were female, that

377   may be a potential factor that might affect the present results, in that female common

378   marmosets are quite sensitive to reciprocity and its violation. However, our previous studies

379   on third-party evaluations included male common marmosets. In addition, no studies on

380   third-party evaluation in primates have suggested potential sex differences. Further studies

381   should examine whether any sex differences exist by including both sexes.

382   In this study, there is one obvious procedural difference between the two conditions, in

383   that the non-reciprocator *A* turned her back on the reciprocating actor *B*, but neither actor

384   moved in the other context and nor did actor *B* in the non-reciprocating condition. Therefore,

385   the monkeys could have been responding to the fact that actor *B* failed to share, or to the fact

386   that actor *B* moved/turned her back, which would have attracted their attention and potentially

387   have been very aversive. The monkeys may have simply reacted to a refusal to share food.

388   However, these refusal gestures have been adopted in previous studies (Anderson et al., 2013;

389   2016). Even more exaggerated gestures were adopted in studies with chimpanzees on a

390   third-party recognition test. Human actors who interrupted giving food to apes and did not

391   merely refuse to donate food to another individual, had negative behaviours including

392   aggression (Russell et al., 2008) and teasing (deliberately holding food out of the beggar's

393   reach; Subiaul et al., 2008) directed at them. These exaggerated behaviours might have

394   influenced the apes' reactions to the actors. Therefore, Anderson and colleagues modified the

395   non-reciprocal exchanges as used in their present study (Anderson et al., 2013). Nevertheless,

396   there may be a possibility that the common marmosets had responded to these gestures or

397   simply reacted to a refusal to share food. However, in either case, the Japanese macaques

398   were not sensitive to such gestures or the event.

399   In summary, our comparative demonstrations successfully replicated third-party

400   evaluations in common marmosets and further revealed no similar evidence for Japanese

macaques. Together with the previous findings regarding third-party evaluations, we have now updated both lists of third-party evaluators (humans, chimpanzees, capuchins, and common marmosets) and low social evaluators (gorillas, orangutans [Herrmann et al., 2013, but see Russell et al., 2008], and Japanese macaques). The boundaries for such social evaluators likely correspond to the differences in their 'socialities' in different aspects (e.g. cooperators or not, tolerant or not, or despotic or egalitarian). Importantly, these boundaries are not always associated with phylogenetic relatedness, but rather likely match with social structures, thereby suggesting the possible evolutionary mechanisms for the convergences of third-party evaluation as an analogous trait. To test whether it has roots in common ancestral primates as a homologous psychological trait within primate lineages, we need more species with a wide range of social structures, especially Old World monkeys. Only in this way will we obtain accurate conclusions regarding the evolutionary origins of social evaluations typically found in human social communication.

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564

564

Figure Captions

Figure 1. An illustration of procedures. In the reciprocal condition (picture on the left), actor *A* took food-B from actor *B*. Next, actor *B* took food-A from actor *A*. Thus two types of food were exchanged between *A* and *B*. In the non-reciprocal condition (picture on the right), actor *A* took food-B from actor *B*. Actor *A* did not allow *B* to take actor *A*'s food. Thus, *A* ended up with four pieces of food and *B* with none. The numbers represent the order of a sequence in an exchange.

Figure 2. Proportion of monkeys' food acceptance from actor *A* and *B* in each condition. The asterisks show significant differences. The vertical bars represent standard errors. The plus shows marginally significant difference.

Legends of supplementary online materials

S1. Raw output of the parameter estimation table in the result of generalized linear mixed model (the estimated best model) fitted by "glmer" method in the "lmer4" and "lmerTest" packages.

The table listed the estimated parameters in the best model. The table was the raw output computed by calling "summary()" function in the R. In this model, Intercept was set at the non-reciprocal condition and marmoset subject. Therefore, "condition_sReciprocal", "sppjm", and "condition_sReciprocal:sppjm" mean the effect of reciprocal condition, Japanese monkeys, and its interaction, respectively. The "Pr" means the probabilities that the estimated parameter differed from 0. In this case, all estimated parameters significantly differed from 0, suggesting the all fixed effect terms showed the statistically significant effects.

S2. Results of model selections by "dredge" method in the "MuMIn" packages.

The all evaluated models listed and ranked by Akaike Information Criterions (AICs). The top line is the best model, the lowest AIC model. The model selection started from the full models, including the possible fixed effect terms, i.e., condition (shown as "condition_s"), session orders ("session_id"), trial orders ("trial_id"), species ("spp") and the random effect term of subject ("subject"). The interaction effect terms were represented as the connection by ":", i.e., "cnd_s:spp" represented the interaction effect term of condition x species. In these models, the intercept was set at the 1st trial of the 1st seeeion in the non-reciprocal condition and marmoset subject. The "(Int)" means the estimations of intercept of the model. The "+" means positive effect of the estimated parameters in the model. For example, the positive effect of "cnd_s" (cnd_s = +) means that choice binary response data was greater in reciprocal condition than in non-reciprocal condition. Likewise, the positive effect of species means that the choice binary response data was greater in Japanese monkeys than in marmosets. The

"df"s were the degrees of freedom for each model, "logLik" were log likelihood of the model, and "delta" were differences of the AICs from the best model.

Fig. 1

Marmoset monkeys

Japanese monkeys

Fig. 2

```
                             Estimate Std. Error z value  Pr(>|z|)
(Intercept)                   -0.3791     0.1046  -3.625 0.0002885
condition_sReciprocal          0.4790     0.1465   3.269 0.0010777
sppjm                          0.4172     0.1393   2.996 0.0027383
condition_sReciprocal:sppjm   -0.4666     0.1958  -2.383 0.0171595
```
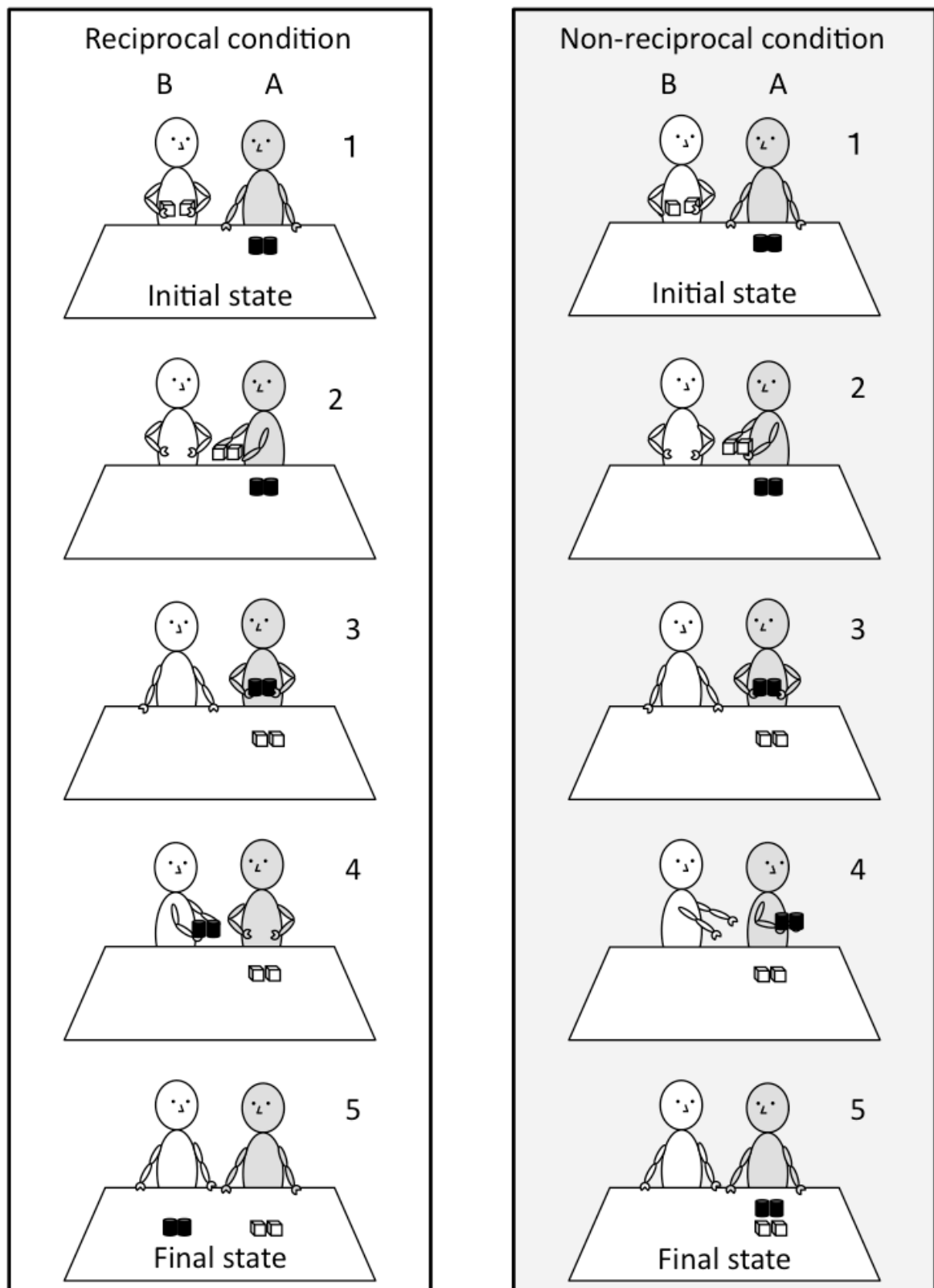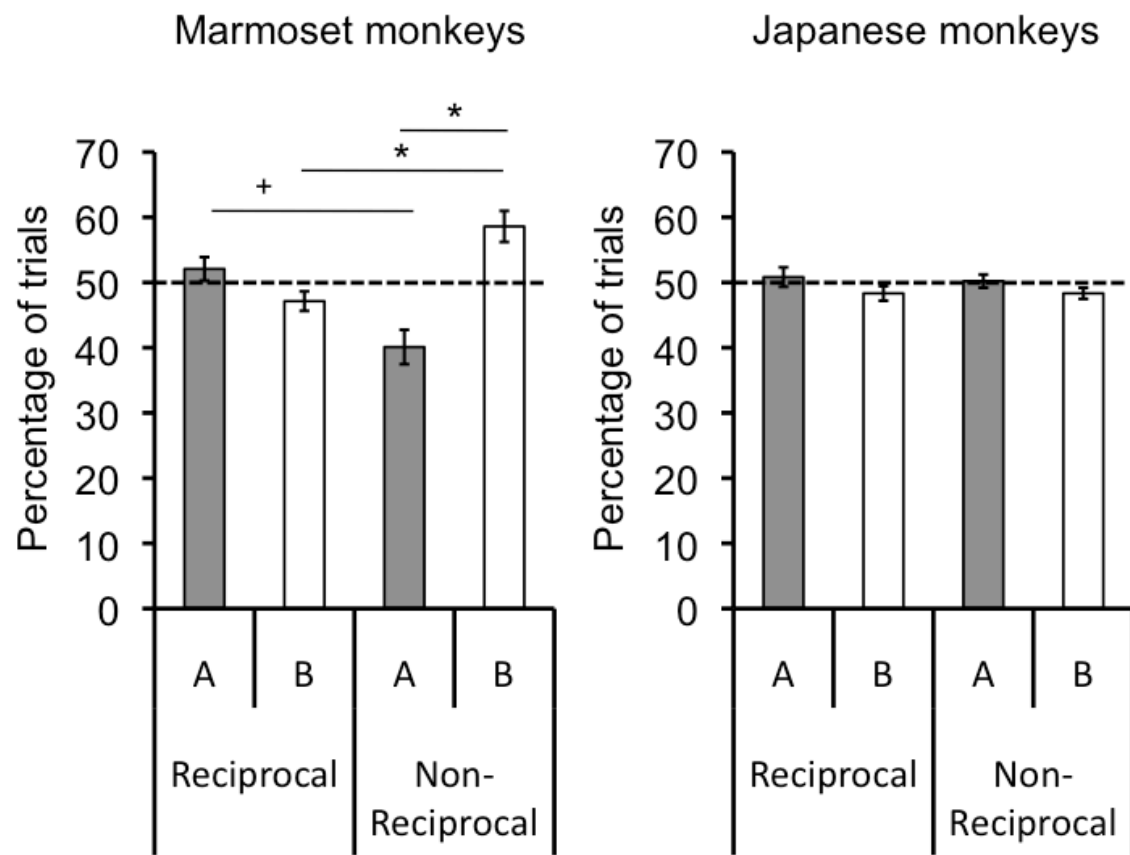
S1

Global model call: glmer(formula = choice ~ condition_s * session_id/trial_id *
    spp + (1 | subject), data = all_data_na_omit, family = binomial(link = logit))

Model selection table

	(Int)	cnd_s	sss_id	spp	cnd_s:sss_id	cnd_s:spp	sss_id:spp	cnd_s:sss_id:spp	cnd_s:sss_id:trl_id	cnd_s:sss_id:spp:trl_id	df	logLik	AIC	delta	weight
22	-0.37910	+		+		+					5	-1177.188	2364.4	0.00	0.372
24	-0.40900	+	0.006603	+		+					6	-1177.139	2366.3	1.90	0.144
32	-0.30920	+	-0.015520	+	+	+					7	-1176.605	2367.2	2.83	0.090
6	-0.24700	+		+							4	-1180.034	2368.1	3.69	0.059
56	-0.41360	+	0.007624	+		+	+				7	-1177.138	2368.3	3.90	0.053
128	-0.12900	+	-0.055770	+	+	+	+	+			9	-1175.179	2368.4	3.98	0.051
64	-0.31310	+	-0.014660	+	+	+	+				8	-1176.604	2369.2	4.83	0.033
160	-0.30960	+	-0.037040	+	+	+			+		9	-1175.613	2369.2	4.85	0.033
2	-0.14580	+									3	-1181.770	2369.5	5.16	0.028
8	-0.27650	+	0.006532	+							5	-1179.987	2370.0	5.60	0.023
256	-0.12870	+	-0.077710	+	+	+	+	+	+		11	-1174.174	2370.3	5.97	0.019
16	-0.17750	+	-0.015440	+	+						6	-1179.453	2370.9	6.53	0.014
5	-0.13710			+							3	-1182.576	2371.2	6.78	0.013
192	-0.31360	+	-0.036140	+	+	+	+		+		10	-1175.612	2371.2	6.85	0.012
4	-0.17520	+	0.006519								4	-1181.722	2371.4	7.07	0.011
40	-0.20000	+	0.007311	+		+					6	-1179.986	2372.0	7.60	0.008
12	-0.07619	+	-0.015450	+							5	-1181.187	2372.4	8.00	0.007
1	-0.03628										2	-1184.307	2372.6	8.24	0.006
48	-0.18070	+	-0.014730	+	+		+				7	-1179.452	2372.9	8.53	0.005
144	-0.17760	+	-0.036410	+	+				+		8	-1178.469	2372.9	8.56	0.005
7	-0.16580		0.006373	+							4	-1182.530	2373.1	8.68	0.005
512	-0.12880	+	-0.073060	+	+	+	+	+	+	+	13	-1174.162	2374.3	9.95	0.003
140	-0.07588	+	-0.036100	+	+				+		7	-1180.218	2374.4	10.06	0.002
3	-0.06492		0.006360								3	-1184.262	2374.5	10.15	0.002
176	-0.18090	+	-0.035690	+	+		+		+		9	-1178.469	2374.5	10.56	0.002
39	-0.16900		0.007098	+		+					5	-1182.530	2375.1	10.68	0.002

Models ranked by AIC(x)
Random terms (all models):
'1 | subject'

S2